Cyclic variation in seasonal recruitment and the evolution of the seasonal decline in Ural owl clutch size

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Plastic life-history traits can be viewed as adaptive responses to environmental conditions, described by a reaction norm. In birds, the decline in clutch size with advancing laying date has been viewed as a reaction norm in response to the parent's own (somatic or local environmental) condition and the seasonal decline in its offspring's reproductive value. Theory predicts that differences in the seasonal recruitment are mirrored in the seasonal decrease in clutch size. We tested this prediction in the Ural owl. The owl's main prey, voles, show a cycle of low, increase and peak phases. Recruitment probability had a humped distribution in both increase and peak phases. Average recruitment probability was two to three times higher in the increase phase and declined faster in the latter part of the season when compared with the peak phase. Clutch size decreased twice as steep in the peak (0.1 eggs day⁻¹) as in the increase phase (0.05 eggs day⁻¹). This result appears to refute theoretical predictions of seasonal clutch size declines. However, a re-examination of current theory shows that the predictions of modelling are less robust to details of seasonal condition accumulation in birds than originally thought. The observed pattern can be predicted, assuming specifically shaped seasonal increases in condition across individuals.

Keywords: life history; seasonal recruitment; reaction norm; clutch size–laying date trend; Ural owl; *Strix uralensis*

1. INTRODUCTION

In most bird species that breed in temperate regions, clutch size declines seasonally (Klomp 1970; Murphy & Haukioja 1986). This has been explained as an individual adaptive response. The optimal clutch size declines through the breeding season because first-winter survival and local recruitment of offspring decreases throughout the season (Hussell 1972; Murphy 1986; Drent & Daan 1980; Daan *et al.* 1990; Daan & Tinbergen 1997). Rowe *et al.* (1994) have provided a general analysis for such seasonal life histories, based on the framework of Daan *et al.* (1988). Parents face a territory-specific gain in condition as the season advances, but territories differ in their initial food supply or the rate of gain in condition. The optimal solution is to produce larger clutches at an earlier date in the better territories (Rowe *et al.* 1994; see also Loman 1982; Daan *et al.* 1990). Here, condition forms a state variable (*sensu* Houston & McNamara 1999) on which the consequences of the reproductive decisions are based. Specific interpretations of condition include somatic resources (Daan *et al.* 1988), foraging yield (Daan *et al.* 1990) and potential clutch size (Aparicio 1994).

The clutch size–laying date relationship forms a reaction norm—a conditional response that dictates how many eggs to produce at which laying date (Rowe *et al.* 1994). Such a reaction norm will be the target for natural selection (e.g. McNamara & Houston 1996). Rowe *et al.*

(1994) specifically predicted that the clutch size–laying date relationship should obey a steeper slope the faster the reproductive value of offspring declines with laying date. To our knowledge, this prediction has not been tested empirically. A comparative study would form a possible test of this prediction. However, it is difficult to obtain consistent measurements of the steepness of the gradient in reproductive value across species or populations, which live in different environments and can vary in many of the parameters that Rowe *et al.* (1994) modelled simultaneously.

As an alternative to comparative tests across species, we can use data on species living in predictably varying environments. Cyclic environments provide a unique opportunity to test hypotheses of clutch-size evolution because differences in seasonal recruitment are likely to occur in such environments. Such an environment is experienced, for example, by birds of prey in the boreal zone that prey on small mammals (mainly voles), which often vary cyclically in their population numbers (Norrdahl 1995). It has been shown that the first-winter survival varies greatly according to the phase of this cycle in several birds of prey, e.g. Tengmalm's owl *Aegolius funereus* L. (Korpimäki 1988), great horned owl *Bubo virginianus* Gmelin (Rohner & Hunter 1996), Ural owl *Strix uralensis* Pall. (Brommer *et al.* 1998) and kestrel *Falco tinnunculus* L. (Korpimäki & Wiehn 1998).

In this paper, we use long-term data on the reproduction and local recruitment of the Ural owl, a species living in a cyclic environment, to show that the seasonal decline in the local recruitment probability of offspring

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depends on the phase of the cycle. We then investigate the clutch size–laying date relationship in various phases of the cycle. We also re-evaluate the predictions of the Rowe *et al.* (1994) model in the light of the data presented.

2. MATERIAL AND METHODS: THE URAL OWL

During their laying season, Ural owls mainly depend on field voles (*Microtus agrestis* L.) and bank voles (*Clethrionomys glareolus* Schreb.) (Lundberg 1981). In Fennoscandia, voles show a cyclic pattern in their population numbers (Hansson & Henttonen 1985; Hanski *et al.* 1991; Norrdahl 1995). The vole cycle is regionally fixed, and in our study area it follows a three-year cycle (Pietiäinen 1989; Brommer *et al.* 1998). The vole cycle is thought to be driven by mustelid predators (Hanski & Korpimäki 1995), and can be considered as an external environmental fluctuation from the Ural owl's perspective. Both sexes of the Ural owl are strictly territorial and highly site-tenacious (only 4% move > 5 km; Saurola 1987). Furthermore, the Ural owl is rather long lived, with an average age at first breeding of 2.9 years and an average breeding lifespan of 3.3 years (Brommer *et al.* 1998). The Ural owl thus lives long enough to gain experience with the three-year vole cycle during its lifetime.

Ural owls were studied in an area of 1500 km² in southern Finland during 1981–1998. All pairs bred in boxes ($n = 155$), which were 3–4 km apart. Any female with at least one egg was classified as a breeding attempt (a nest). Laying date was determined either by a visit to a nest with an incomplete clutch or by backdating from nestling wing lengths (see Pietiäinen (1989) for more details). Laying dates were standardized with the long-term median (31 March), thus 1 April = 1 and 21 March = –10. The number of fledglings was calculated as the number of 3–4-week-old young. Females were netted from the box during laying or incubation. Males were trapped using a trap attached to the box in the first week after the offspring hatched.

For analyses of recruitment of offspring, we used all individuals that were recorded as breeding later in life, both within and outside the study area. Both females and males were included, although few Finnish ringers trap males. Because 76% of first-breeders started within 3 years after fledging (Brommer *et al.* 1998), we used only data until 1998 so that birds had the possibility of being controlled as a breeding adult during the study period. These estimates do not describe an absolute probability of recruitment because the vast majority of birds are probably not available for quantitative studies on recruitment (Lambrechts *et al.* 2000), but they provide us with a relative measure, which can be used for comparison between and within years.

Because we are interested in relating the seasonal decrease in offspring reproductive value to the seasonal decline in Ural owl clutch size, we considered the per-egg recruitment probability as a proxy for an egg's reproductive value. Seasonal local recruitment probability was analysed by logistic regression on the number of recruited offspring produced per laying date and phase, with the number of eggs (or fledglings) used as the binomially distributed denominator. The minimal adequate model was found by deleting insignificant explanatory variables, starting with the highest-order interaction (Crawley 1993). We tested whether the difference in the seasonal decline of local recruitment in increase and peak phases was reflected in the seasonal decline of clutch size by using ANOVA on two levels: the indi-

vidual level and the population level. On the individual level, we considered only females which bred at least once in an increase and a peak phase. We randomly selected one breeding record per increase and one per peak phase for each of these females to avoid pseudo-replication. On the population level, we considered one randomly selected breeding record of all females. The intercept (a) and slope (b) of the seasonal decline in their clutch size were estimated by linear regression.

3. RESULTS

Local recruitment was analysed from both the egg stage and the fledgling stage. In the low phases, 144 eggs (113 fledglings) out of 63 nests produced one recruit (0.7% of eggs). In the increase phases, 1212 eggs (956 fledglings) out of 338 nests produced 74 recruits (6.1% of eggs). In the peak phases, 1259 eggs (921 fledglings) out of 345 nests produced 21 recruits (1.7% of eggs). We analysed only the seasonal local recruitment for increase and peak phases because only one egg hatched in a low phase recruited later in life.

The seasonal local recruitment probability showed a bumped distribution in both phases (figure 1, table 1). The phases differed in both the position and the height of the maximum local recruitment probability of the logistic fitted: maximum local recruitment probability in the increase phase was after the average laying date ('0' in figure 1), but before the average laying date in the peak phase (table 1, figure 1). Furthermore, the seasonal maximum in local recruitment probability was about three times higher for offspring that hatched in an increase phase than for offspring that hatched in a peak phase. The earliest and the latest eggs produced in both phases had the lowest local recruitment probabilities. Nevertheless, the earliest broods in the increase phase (figure 1a) still had a probability to recruit that was equal to the maximum local recruitment probability in the peak phase (ca. 2.5%; figure 1). The local recruitment probability of fledglings showed qualitatively the same seasonal pattern as for eggs (phase $\times$ laying date²: $\Delta D = 1.7$, $p = \text{n.s.}$; phase $\times$ laying date: $\Delta D = 4.2$, $p = 0.04$; laying date²: $\Delta D = 6.2$, $p = 0.01$). In conclusion, local recruitment probability declined faster in the increase phases than in the peak phases, at least for the latter half of the breeding season.

During the same study period, 121 females bred in at least one increase and one peak year. The rate of the seasonal decrease in clutch size of these females differed between the increase and peak phases of the vole cycle (figure 2). In the peak phase, clutch size decreased twice as fast with advancing laying date (a : 3.2 ± 0.08 ; b : -0.10 ± 0.008 eggs day⁻¹) as in the increase phase (a : 3.7 ± 0.07 ; b : -0.05 ± 0.009 eggs day⁻¹). The owls started reproducing at a later date in the increase phase than in the peak phase (figure 2), which is consistent with the maximum in local recruitment probability being later in the increase phase than in the peak phase (figure 1). For later laying dates, the difference in the elevation and the rate of decrease in clutch size between the phases led to the production of larger clutches in the increase years than in peak years on the same laying date (figure 2). A total of 272 females bred in the study area during the study period. Qualitatively the same pattern was found

Figure 1. Local recruitment of offspring as categorized by date and phase of hatching. The data are presented as the local recruitment probability for an egg for each laying date of the first egg in the clutch. The solid lines represent the fitted logistic regression (table 1). Lines are drawn over the observed range in laying dates. For a clearer representation, a slight random jitter was added to the points at which local recruitment probability was zero. The local recruitment probability p , as estimated by the logistic regression model m , was plotted as the function $p = e^m / (1 + e^m)$. For significance and coefficients of these models, see table 1. The logistic function for the local recruitment probability of fledglings is qualitatively the same.

Table 1. Stepwise backwards logistic regression on the local recruitment probability for date and phase.

(Local recruitment probability is estimated as the number of recruits per date and per phase, with the number of eggs produced per date and per phase as the binomially distributed denominator. Only increase and peak phase were included, where the phases were dummy coded (increase, 0 and peak, 1). The deviance D of the null model (constant and phase) and the minimal adequate model (variables listed) is given (null versus minimal adequate model: $\Delta D = 7.7$, $\Delta \text{d.f.} = 3$, $p = 0.06$). The effect of each variable is tested by a χ^2 test of the change in deviance (ΔD) and change in degrees of freedom ($\Delta \text{d.f.}$) in the model when a particular variable is not included. The variable with the lowest (non-significant) effect is dropped, starting with the highest-order interaction.)

variable	coefficient	(Δ) D	(Δ)d.f.	p
null model		80.1	93	0.83
minimal adequate model		72.4	90	0.91
constant	-2.5 ± 0.14			
phase	-1.5 ± 0.35			
laying date	0.025 ± 0.018			
laying date ²	-0.0034 ± 0.0015	7.3	1	0.01
phase $\times$ laying date	-0.081 ± 0.045	3.8	1	0.05
dropped variable(s)				
phase $\times$ laying date ²	-0.006 ± 0.005	1.8	1	0.18

when analysing the population-wide data (one breeding record per female, all phases included: $F_{1,266} = 40.8$, $p < 0.001$; phase: $F_{2,266} = 7.0$, $p = 0.005$; phase $\times$ date: $F_{1,266} = 8.6$, $p = 0.001$, $r^2 = 0.43$; low: $a = 2.9 \pm 0.07$, $b = -0.05 \pm 0.02$, ($n = 7$), increase: $a = 3.6 \pm 0.07$, $b = -0.04 \pm 0.008$, ($n = 120$), peak: $a = 3.4 \pm 0.08$, $b = -0.08 \pm 0.008$, ($n = 135$)). Furthermore, this phenomenon was not a result of individuals adjusting their reproductive behaviour in response to their previous experience because first-breeders, which have no prior breeding experience, also showed the same pattern (date: $F_{1,189} = 78.9$, $p < 0.001$; phase: $F_{1,189} = 3.9$; $p = 0.05$; phase $\times$ date: $F_{1,189} = 8.5$, $p = 0.004$, $r^2 = 0.34$; increase: $a = 3.6 \pm 0.07$, $b = -0.04 \pm 0.008$, ($n = 124$), peak: $a = 3.4 \pm 0.10$, $b = -0.08 \pm 0.01$, ($n = 69$)).

4. INTERPRETATION: WHAT DOES THE THEORY PREDICT?

In this section, we review and re-evaluate the argumentation of Daan *et al.* (1988) and Rowe *et al.* (1994). Ori-

ginally, their predictions were based on the idea that eggs are formed from a 'capital' $C(t)$ of accumulated energy resources (*sensu* Drent & Daan 1980; Jönsson 1997). These resources then determine the potential clutch size (e.g. Aparicio 1994). More generally, however, $C(t)$ represents the key variable in a condition-dependent setting, where the consequences of all reproductive actions (laying date and clutch size) are dependent on (Houston & McNamara 1999). Likewise, $C(t)$ could refer to (expected) foraging yield (Daan *et al.* 1990; Daan & Tinbergen 1997). The theory could therefore also apply to income breeders, such as passerines, which time their breeding in response to local food abundance (e.g. Van Noordwijk *et al.* 1995; Thomas *et al.* 2001), where $C(t)$ refers to local environmental (territorial) conditions. In fact, we may view $C(t)$ as any function that is positively related to offspring production, describing, for example, the increase in somatic size (e.g. Stearns & Koella 1986; Rowe *et al.* 1994). Here, we simplify the model by Rowe *et al.* (1994) by equating condition $C(t)$ with the clutch size that the parent can lay at time t .

Figure 2. The clutch size–laying date for 121 females, which bred in at least one increase and one peak phase. Only one nest per individual in an increase and in a peak phase was included. Clutch size declined as the season advanced but did so at a faster rate in the peak phase (date: $F_{1,238} = 159.6$, $p < 0.001$; phase: $F_{1,238} = 20.4$, $p < 0.001$; phase $\times$ date: $F_{1,238} = 18.8$, $p < 0.001$, $r^2 = 0.45$). Clutches produced in the peak phase are indicated by circles and increase phase by squares. To aid in comparison of clutch size categories produced at the same laying date, clutch sizes in the peak phase are plotted above those produced in the increase phase. The lines drawn are the fitted regressions for each phase. These lines were calculated for the original data and are drawn over the observed range of laying dates. Peak phase is indicated by a solid line and increase phase by a dashed line.

Conditions accumulate differently for different parents, due to variation in the qualities of their territories. Laying date and clutch size are determined by a solution to a trade-off between benefits and costs of laying at a certain time. The parent can lay more eggs if it delays laying, as its condition improves through time, due to, for example, an increase in the abundance of food; hence, $C(t)$ is increasing. Conversely, the reproductive value $V(t)$, of which local recruitment probability is a major determinant (Daan *et al.* 1990; see Brommer *et al.* (2000) for a dynamic model) declines as the season advances. Parents are selected to choose the laying date t^* to maximize the sum of reproductive values of offspring (Houston & McNamara 1999), i.e. maximize $C(t)V(t)$. It follows that t^* must satisfy

$$\left(\frac{dC}{dt} V(t) + C(t) \frac{dV}{dt} = 0 \right) \bigg|_{t=t^*} \Leftrightarrow \frac{C'(t)}{C(t)} = - \frac{V'(t)}{V(t)} \bigg|_{t=t^*}. \quad (4.1)$$

This relationship is the essence of the model of Rowe *et al.* (1994). The optimal timing for laying is the t^* at which the costs of delaying (the relative decline in offspring value, $V'(t)/V(t)$) are exactly offset by the benefits of delaying (the relative increase in the number of young that can be produced, $C'(t)/C(t)$). The relative decline in offspring value, $V'(t)/V(t)$, is an increasing function of t for almost all decreasing functions of offspring reproductive value $V(t)$. Delay is always optimal when $V(t)$ is

increasing because an individual then gains both a higher potential clutch size and a higher reproductive value of its offspring. Hence, in a theoretical interpretation of the Ural owl's humped distribution of seasonal local recruitment probability (figure 1) as a parameterization of $V(t)$, we may focus on the decreasing part of the curves.

From condition (4.1), Rowe *et al.* (1994) make the following assertion. If offspring reproductive value declines faster, $V'(t)/V(t)$ increases. Due to the shape of the $C'(t)/C(t)$ curve (fig. 1 in Rowe *et al.* 1994), this would result in a steeper relationship between clutch size and laying date. Our results on the Ural owl do not support this prediction of Rowe *et al.* (1994) if we use local recruitment probability as a proxy for offspring reproductive value $V(t)$. In increase years of the vole cycle, offspring value decreases more rapidly as the season advances than in peak years, but—contrary to what was predicted—increase years showed a shallower clutch size–laying date relationship than peak years.

Nevertheless, we find the graphical approach of Rowe *et al.* (1994) partially problematic. First, the argument of a steeper slope in the $V(t)$ function resulting in a higher $V'(t)/V(t)$ is not robust with respect to the starting value of $V(t)$ early in the season. For example, if we assume that the reproductive value of offspring decreases linearly as $V(t) = V_0 - \beta t$, a steeper slope (higher β) will only result in a higher $V'(t)/V(t)$ if the initial value V_0 is altered less than β was. There is, however, no biological reason for assuming that V_0 would remain constant if β is changed. This is illustrated by the data on the Ural owl, in which local recruitment probability in the increase phase has a higher maximum (higher V_0) and also falls off steeper than in the peak phase.

Second, horizontal lines in Rowe *et al.*'s (1994) fig. 1 connect points for which $C'(t)/C(t) = -V'(t)/V(t)$. A shift in the location of the $V'(t)/V(t)$ curve may cause a steeper decline in clutch size if laying dates t^* remain unchanged. However, when $V'(t)/V(t)$ changes, the optimal dates t^* may themselves shift, which will alter the location of solutions on the $C'(t)/C(t)$ curve, possibly in a way that allows for a shallower relationship between laying date and clutch size when $V'(t)/V(t)$ is large. This makes the range of solutions more variable than Rowe *et al.* (1994) indicate. We illustrate this problem with two specific examples. Throughout, we assume that the reproductive value of offspring decreases linearly as $V(t) = V_0 - \beta t$, which is the same for all parents.

(a) Example 1

Assume that individual condition increases as

$$C(t) = C_0 + \alpha t \quad (4.2)$$

(see also Loman 1982; Daan *et al.* 1990). Initial condition C_0 at $t = 0$ varies among individuals, whereas condition is assumed to increase at the same rate α for all individuals. These assumptions correspond to the case considered by Rowe *et al.* (1994). Applying condition (4.1) gives

$$C_0 + \alpha t^* - \alpha \frac{V_0}{\beta} + \alpha t^* = 0, \quad (4.3)$$

and by inserting equation (4.2) into equation (4.3), the optimal clutch size–laying date $C^*(t^*)$ relationship is expressed as

$$C^*(t^*) = \alpha \frac{V_0}{\beta} - \alpha t^*. \quad (4.4)$$

Regardless of the baseline reproductive value V_0 or its rate of decrease β , the slope of the clutch size–laying date relationship is $-\alpha$ (equation (4.4)). Optimal timing for particular sets of C_0 is then determined by

$$t^* = \frac{V_0}{2\beta} - \frac{C_0}{2\alpha}$$

and the optimal clutch size by

$$C^* = \frac{C_0}{2} + \alpha \frac{V_0}{2\beta}.$$

Figure 3a shows an example between the optimal lay dates and clutch sizes for a range of individual conditions C_0 . Hence, when assuming linear changes in condition and in reproductive values of offspring, the rate at which reproductive value declines over the season has no impact on the optimal clutch size–laying date relationship (figure 3a). In terms of the Ural owl's life history, this example would predict that increase years of the vole cycle have the same clutch size–laying date slope as peak years.

(b) Example 2

Assume that condition of the birds peaks at t_m at value C_m and increases before that in a decelerating fashion, thus

$$C(t) = C_m - \gamma(t - t_m)^2, \quad (4.5)$$

where γ is a parameter that scales the rate of condition increase, and is assumed to be constant and equal for all territories in all seasons. Note that this is a more general function than allowed by Rowe *et al.* (equation (1) in Rowe *et al.* 1994), as the rate of increase in condition $C'(t)$ depends on time t independently of condition. Applying relationship (4.1) and inserting equation (4.5), the optimal clutch size–laying date relationship can be expressed as

$$C^*(t^*) = 2\gamma \left((t^*)^2 - \left(\frac{V_0}{\beta} + t_m \right) t^* + \frac{V_0}{\beta} t_m \right). \quad (4.6)$$

It becomes optimal to reproduce later in the season and the relationship's slope will become steeper with a larger ratio V_0/β as $C^*(0)$ increases proportionally to V_0/β , but the minimum at $t^* = 1/2(V_0/\beta + t_m)$ does not. Equation (4.6) can be solved analytically to derive the optimal laying dates t^* and the corresponding optimal clutch size $C^*(t^*)$ for a given set of C_m . An example is given (figure 3b), where the ratio V_0/β is increasing from 4.7 (triangles) to 6.7 (squares) to 10 (circles), and the clutch size–laying date becomes steeper. Assuming that γ and t_m remain unchanged between phases, note that t^* becomes both later and less widely spaced out, which was not incorporated in the graphical analysis of Rowe *et al.* (1994).

What does this model predict for an increase year versus a peak year? In the increase year, local recruitment probability is high, which means a large V_0 , but the slope is also steep (large β). We can, without loss of generality, consider only the latter, declining part of the recruitment probability function in figure 1 as an estimate of the function $V(t)$. For simplicity, we further consider the decrease

Figure 3. Model predictions for examples 1, 2 and 3, illustrating that a steep slope β or a high baseline reproductive value V_0 of offspring can render the clutch size–laying date relationship either steeper, shallower, or have no effect. In each case, the offspring's value declines linearly ($V(t) = V_0 - \beta t$). The triangles form a basic example, squares are obtained by increasing the reproductive value V_0 and circles by additionally decreasing β . Parameter values: $V_0 = 0.7$ (triangles) or 1 (squares, circles), $\beta = 0.15$ (triangles, squares) or 0.1 (circles). Solutions are plotted for C_0 (example 1), C_m (example 2) or C_q (example 3) varying from 0.5 to 4.5 with step size 0.5. (a) Example 1 assumes a linear increase in condition, $\alpha = 1$. V_0 or β have no effect on the slope. (b) Example 2 assumes decelerating condition gain, $\gamma = 1$, $t_m = 5$. Higher baseline reproductive value (high V_0) or shallower decline in reproductive value (low β) causes a steeper relationship of clutch size versus laying date. (c) Example 3 assumes that birds with higher initial condition approach peak condition more quickly, $C_m = 6$, $f = 0.25$, $\delta = 1$. Higher baseline reproductive value (high V_0) or shallower decline in reproductive value (low β) causes a shallower relationship of clutch size versus laying date. Variation between the examples in the scales on the axes is due to differences in the scales of condition gain, which are arbitrary and simply chosen to produce clear examples.

in local recruitment probability from the maximum recruitment to 0.5% recruitment probability as linear because the optimization argument (equation (4.1)) is

robust to the precise shape of the decline (Rowe *et al.* 1994). In the increase phase, local recruitment declines from a maximum of 7.8% to 0.5% in 28 days (day 3 to 31 in figure 1*a*) and in the peak phase from 2.2% to 0.5% in 20 days (day -8 to 12 in figure 1*b*). The ratio V_0/β is thus about 16% higher in the increase phase than in the peak phase, and a condition gain according to equation (4.5) would then predict a steeper clutch size-laying date slope in the increase phase compared with the peak phase (figure 3). However, the clutch size-laying date observed in the Ural owl shows the opposite pattern (figure 2).

Contrary to Rowe *et al.* (1994), equation (4.6) predicts that the clutch size-laying date slope becomes steeper if recruitment falls off less steeply with time (or, more precisely, if the ratio V_0/β increases). An intuitive explanation is as follows. If the reproductive value of offspring is largely independent of the timing of their production, all birds should produce young late in the season because they lose little by doing so. With our choice of the condition gain $C(t)$, all birds approach their individual maximum condition C_m near the end of the season. Consequently, condition at laying varies significantly among individuals, whereas timing varies only little (although individuals in best condition still lay earliest). This generates a steep slope of clutch size versus laying date. In the extreme case of no seasonal decrease in offspring's reproductive value $V(t)$, the slope is vertical as all clutches are produced at the seasonal maximum in condition at $t^* = t_m$ (see also fig. 13.10 in Daan & Tinbergen 1997). However, if the reproductive value of offspring falls off quickly as the season progresses, parents should reproduce as soon as they can produce a sufficiently large clutch size to maximize $C(t)V(t)$. This happens much earlier for individuals in better condition, and more spaced out timing produces a shallower clutch size-laying date relationship.

Continuing this line of reasoning, however, makes it clear that solutions can be constructed where slopes indeed become steeper when reproductive values fall off quickly with time. This is illustrated by the following example.

(c) Example 3

Assume that birds achieve a territory-specific maximum in condition but birds with a higher initial condition approach this maximum more quickly, i.e. $C'(t)$ depends both on time t and a territory-specific parameter C_q . One example is provided by the exponential function

$$C(t) = C_m - fC_q - \exp(-\delta[t - C_q]), \quad (4.7)$$

where a higher C_q lowers both the asymptotic maximum ($C_m - fC_q$) and the rate at which this territory-specific maximum is approached. The degree with which C_q lowers the maximum condition is further scaled by a fraction f . When $f = 0$ all territories will approach maximum C_m , and for $f > 0$, territories with a lower initial condition $C(0)$ will also have a lower maximum. The parameter δ further scales the seasonal rate of increase in condition. The optimal laying dates t^* can be solved numerically and they reveal a pattern in which increasing V_0 and decreasing β produces shallower slopes (figure 3*c*). Intuitively, if individuals vary mainly in their timing of approaching peak condition but less so in the height of the peak, and

reproductive values of offspring do not significantly decline over the season, all individuals will produce roughly equal clutch sizes but at different times. Hence, in this case, the clutch size-laying date slope will be shallow when the reproductive value of offspring declines slowly over time.

5. DISCUSSION

The ubiquitous phenomenon of a seasonal decrease in clutch size in birds is thought to form a reaction norm in response to variation in the seasonal gain of parental condition and a seasonal decrease in offspring's reproductive value (Drent & Daan 1980; Loman 1982; Daan *et al.* 1990; Aparicio 1994; Rowe *et al.* 1994; Brinkhof & Cavé 1997; Daan & Tinbergen 1997). A reaction norm describing the relationship between a temporal trait (e.g. age at maturation or laying date) and a reproductive component (e.g. size at maturation or clutch size) is typically visualized as a single-switch curve (e.g. Stearns & Koella 1986; Meijer *et al.* 1990). Such a single-switch curve implies that the reproductive decisions of all individuals follow this curve and that this curve is the norm for each year. The concept of the clutch size-laying date relationship as such a reaction norm can be tested at several levels. For example, Meijer *et al.* (1990) argued for a rigid causal chain between food supply, laying date and clutch size, because supplemental feeding of kestrels in The Netherlands induced both earlier laying dates and corresponding larger clutches (but see Aparicio 1994; Korpimäki & Wiehn 1998). Our study takes advantage of predictable variation in the environment experienced by breeding owls. The Ural owl is both highly site-tenacious and long lived, which allows us to verify the theoretical prediction of Rowe *et al.* (1994) concerning the covariation of seasonal recruitment and the seasonal decline in clutch size. This prediction is based on modelling of parental reproductive decisions in response to a territory-specific increase in condition and a general seasonal decline in the reproductive value of offspring. We have shown that the seasonal local recruitment probability of Ural owl offspring declines at different rates in different phases of the vole cycle, and that the slope of the seasonal decline of Ural owl clutch size in these phases is inversely related to the decline in local recruitment probability.

In the increase phase, when food availability is stable or even increasing, offspring survival and, consequently, local recruitment is generally high (Brommer *et al.* 1998). However, both early- and late-hatched offspring experience reduced recruitment chances. In the peak phase, later-hatched offspring suffer even more from the rapidly deteriorating food conditions than in the increase phase because the vole populations crash during early summer. Moreover, even at its best, average local recruitment probability of peak-hatched offspring is only about one-third of the local recruitment for increase-hatched offspring. We have, at present, no explanation for the seemingly low local recruitment of the earliest broods in both increase and peak phases. Within-nest mortality of eggs and chicks can be ruled out as a factor behind the poor local recruitment of early broods because the local recruitment of fledglings shows the same pattern as for eggs. Although few empirical studies have addressed variability between

years in recruitment, inter-annual differences in the seasonal recruitment should be typical, although probably not as pronounced as in the Ural owl. For example, Verboven & Visser (1998) found that the slope of the seasonal local recruitment in great tits (*Parus major* L.) differed between years. Such annual variation in the seasonal recruitment is probably not always predictable to the parents. In the case of the Ural owl, however, the existence of a regular three-point cycle creates predictable differences in the (seasonal) recruitment between phases.

The between-phase differences in the seasonal decline of clutch size in the Ural owl provide an empirical illustration that the classical clutch size–laying date relationship is not necessarily fixed each year but can instead be flexible between years of different quality. Rowe *et al.* (1994) predicted that differences in the seasonal decline of reproductive value should be mirrored in the seasonal decline in clutch size. We have presented a review of the theory underlying this phenomenon, in which the shape of the seasonal increase in condition is assumed to be the same each season. Covariation of a decrease in recruitment probability and the seasonal decrease in clutch size may then be expected. However, whether this seasonal decline in clutch size becomes steeper or shallower with a more rapid seasonal decrease in offspring's reproductive value largely depends on the way the potential clutch size, or condition, builds up as the season advances. Furthermore, care should be taken in basing predictions solely on the slope of the seasonal decline in recruitment probability as the elevation (the intercept V_0) also plays a crucial role. The pattern of Ural owl clutch size and laying date in increase and peak phases corresponds with the scenario in which territories differ in their initial condition and in which better territories show a higher rate of increase in condition to their territory-specific maximum. Usually, the seasonal increase in condition is assumed to be linear (Loman 1982; Daan *et al.* 1990; Rowe *et al.* 1994). However, we feel that such a function is not very plausible, as, for example, food typically becomes plentiful everywhere and climatic conditions improve later in spring. The largest between-territory differences may therefore be expected in early spring. Furthermore, there may well be a (physiological) maximum in condition, whether condition is interpreted as body size, food supply, foraging yield or potential clutch size.

Inter-annual differences in the clutch size–laying date relationship have also been observed in the vole-eating Tengmalm's owls in Sweden (Hörmfeldt & Eklund 1990). A Finnish population of this species, which experienced a similar vole cycle as described here, also showed a steeper seasonal decline in clutch size in the peak phases than in the increase phases, but the seasonal recruitment probability is not known in this population (Korpimäki & Hakkarainen 1991). Conversely, kestrels breeding in southwestern Finland experience a similar three-year cycle in their food availability, but do not show differences in their clutch size–laying date relationship between these phases (Korpimäki & Wiehn 1998). In this kestrel population, there are large differences in recruitment probability between phases, but there is no apparent seasonal decline in recruitment in any phase (Korpimäki & Wiehn 1998). Nevertheless, all these studies concern a population-wide seasonal decline in clutch size and concern,

therefore, different sets of birds breeding in the different phases, whereas the theoretical predictions are most conservatively tested on an individual basis. To gain insight into the generality of the idea of a seasonal decrease in clutch size as a response to the seasonal decrease in recruitment, further studies are needed of the relationship between these two patterns. A comparison between species or populations that live in regularly or irregularly varying environments, or those that experience little annual variation, would be especially worthwhile. Nevertheless, to predict changes in clutch size–laying date slopes, it is also essential to know how (somatic and local environmental) conditions increase for different individuals as the season advances. Our study calls for more data to examine this question.

Finally, we point to a limitation of current modelling. All models discussed above ignore the future reproductive value of the parent, which is appropriate if the parental fitness costs per unit effort do not change with lay date. If the parent needs time to recover after breeding or if costs of reproduction are paid either before or after the reproductive period (e.g. Jönsson *et al.* 1995), parental residual reproductive value may decline with the timing of breeding. Nevertheless, such effects have not been demonstrated empirically. In the Ural owl, residual reproductive value may decline more rapidly if the density of prey crashes later in the season (Brommer *et al.* 2000). Alternatively, if breeding that is too early is costly, the parent's residual reproductive value may be lowest when breeding too early. Because the reproductive value of a parent can simply be added to those of its offspring (see Houston & McNamara 1999), such effects can, in a simplifying approach, be incorporated in the choice of the function $V(t)$. However, the issue becomes more complicated if parents can also choose how much parental effort they spend, given a condition and timing $C(t)$. Allowing for such variation would probably further increase the diversity of potential clutch size–laying date relationships.

We received financial support from the Academy of Finland (H.P.), Helsinki School of Conservation and Management of Wildlife Populations graduate school (J.E.B.), Societas pro Fauna et Flora Fennica (J.E.B.), Suomen Kulttuurirahasto (J.E.B.), the Division of Population Biology (J.E.B., H.P.), the TBA programme of the ESF (J.E.B.) and The Royal Society (H.K.). For discussion, we are grateful to Peter E. Brommer, Juha Merilä, Bob O'Hara and Joost M. Tinbergen. The comments of three anonymous referees greatly improved the manuscript.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.